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Meteoriopsis undulata Horik. & Nog. (Bryophyta: Meteoriaceae) new to the Australian flora

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Abstract

Meteoriopsis undulata Horik. & Nog. (Bryophyta: Meteoriaceae), previously known only from Japan, Taiwan and China, is reported as new to Australia from two collections in the Wet Tropics of north-eastern Queensland. A revision of the current Australian moss key is suggested to accommodate this species.

Introduction

The genus *Meteoriopsis* was revised by Manuel (1977) to include only three species from Asia: *M. reclinata* (Müll.Hal.) M.Fleisch. ex Broth., *M. squarrosa* (Hook.) M.Fleisch. ex Broth. and *M. undulata* Horik. & Nog. *Meteoriopsis reclinata* was the only species reported from Australia. *Meteoriopsis undulata* was known at that time only from Japan, but subsequent collections from Taiwan and from Guanxi province in China broadened its distribution (Noguchi 1986, Wu and Lin 1986). A further species, *M. novoguinensis* Nog. from Papua New Guinea, was described by Noguchi (1986).

In May 2015 we collected an epiphytic moss from two locations in the Wet Tropics of north-eastern Queensland: one from a rotting vine (collection no. WT-616) and the other from a tree trunk (WT-637). We identified these in the field as *Isocladiella wattsii* (Broth.) B.C.Tan, H.P.Ramsay & W.B.Schofield because of the presence of long flagelliform branchlets, which was considered a defining character for that species among Australian mosses (Ramsay 2012). We subsequently sent part of WT-637 to Helen Ramsay (Royal Botanic Garden, Sydney). However, after she and Alison Downing (Macquarie University) examined the specimen they pointed out that it belonged in *Meteoriopsis* (Meteoriaceae) and suggested that it might be *Meteoriopsis undulata*.

Morphological assessment

We consequently compared WT-616 and WT-637 with published descriptions of *Meteoriopsis* species and two similar species of Meteoriaceae, *Pseudotrachypus ancistrodes* (Renault & Cardot) V.Nath & Bansal and *Meteorium filiforme* Nog. We also examined authoritatively identified specimens of *Meteoriopsis novoguinensis* (CBG-8307764 and CBG-8307764), *M. undulata* (CBG-8207146), *M. squarrosa* (*Koponen 30732* ex H in MELU) and *P. ancistrodes* (CBG-9504251 and CBG-84051153, as *Pseudobarbella ancistrodes*) available in Australian herbaria, and our own collections of *M. reclinata*.

Our material does not fit within *M. reclinata* nor *M. squarrosa* because its leaf margins are undulate, flagelliform branchlets are present, and the leaves are widely spreading rather than ± squarrose and become gradually smaller towards the apex of branches. *M. novoguinensis* and *P. ancistrodes* were also discounted because of obvious differences in gross morphology: *M. novoguinensis* is a much larger plant than WT-616 and WT-637 and has a more bristly appearance, and the papillae are less distinct, as noted by Noguchi (1986) in comparing it with *M. undulata*. Both *P. ancistrodes* and *M. filiforme* have a trailing habit. In addition, *P. ancistrodes* has much larger stem leaves (to 2.5 mm long), the laminal cells are only rarely bipapillose, and there are no flagelliform branchlets. *Meteorium filiforme* also has much larger stem leaves (to 3 mm long), the laminal cells are entirely unipapillose, the leaf margins are entire rather than denticulate, and the leaves of the secondary filiform branches are broadly ovate, rounded with a shortly acuminate apex.

We concluded that WT-616 and WT-637 did belong in *Meteoriopsis* and best matched *Meteoriopsis undulata*, although flagelliform branchlets were not mentioned by Noguchi (1936) or Manuel (1977). Table 1 shows stem, branch and branchlet leaf measurements of WT-616 and WT-637 against those of CBG-8207146 and published measurements. The gross morphology of WT-637 is very close to that of CBG-8207146, which was collected in Japan by Zen Iwatsuki and Hiroshi Kiguchi and identified by Iwatsuki, with the identification later confirmed by Akira Noguchi. It formed no. 1578 of the Musci Japonii Exsiccati series 32 (1981), edited by Iwatsuki and Noguchi. The following description is based on our Australian material (Figs 1, 2). The locations of our collections are shown in Fig. 3.

Table 1: Morphological measurements of WT-616, WT-637 and CBG 8207146 and published measurements of *Meteoriopsis undulata*.

Character	WT-616 & WT-637	(CBG-8207146)	Noguchi (1936)	Manuel (1977)	Wu and Lin (1986)	Wu and Pei (2011)
Stem length (cm)	8–13	N/A	15	7.5	not mentioned	not mentioned
Stem leaf length (mm)	(1.39–) 1.84–1.91	1.73–2.9	1.8	1.08–2.01	(1.45–) 1.7–2.35 (–2.55)	1.8**
Stem leaf width (mm)	(0.47–) 0.53–0.63	(0.58–) 0.79–0.9	0.6	0.38–1.0	(0.5–) 0.65–0.9 (–1.05)	0.6**
Branch length (mm)	5–7	5–8	5–10	5–10	5–12	5–12
Branch leaf length (mm)	1.6–1.8	(1.27–) 1.72–1.91	1.6	0.9–1.89	0.6–1.25	not mentioned
Branch leaf width (mm)	0.69–0.86	0.51–0.71	0.73	0.39–0.9	0.15–0.25	not mentioned
Branchlet length (mm)	2–14	7–9	not mentioned	not mentioned	c. 10	not mentioned
Branchlet leaf length (mm)	0.4–0.53	0.65–0.82	not mentioned	not mentioned	0.6–1.1*	not mentioned
Branchlet leaf width (mm)	0.09–0.13	0.17–0.2	not mentioned	not mentioned	0.15–0.2*	not mentioned
Lamina cell l × w – stem leaf (μm)	54–64 × 4.5–6.4	41–46 × 5.4–5.9	not mentioned	25.0–32.5 (–45.0) × 3.75–5.0	(25–) 30–60 (–70) × 2.5–5	20–60 × 5–6**
Lamina cell l × w – branch leaf (μm)	41–64 × 6	42–51 × 4.5–6.5	not mentioned	22.5–40.0 × 3.75–7.5	not mentioned	not mentioned
Lamina cell l × w – branchlet leaf (μm)	40–45 × 5–7	37–48 × 2.6–3.9	not mentioned	not mentioned	not mentioned	not mentioned

* Not included in text; estimate from illustration of *M. undulata* in Wu & Lin (1986)

** Not specified whether stem or branch

Meteoriopsis undulata **Horik. & Nog. in Nog., *J. Sci. Hiroshima Univ.* sect. B., div. 2, 3: 16**

TYPE: Holotype (*Noguchi 9400*, Hiroshima University Herbarium) destroyed in World War 2 (*fide* Noguchi, cited in Manuel 1977). Paratypes not extant (*fide* Manuel 1977). Neotype (*fide* Manuel 1977) Japan, Kyushu, Miyazaki-Pref. Nakago-mura, Yasuhisa, *Noguchi 9399*, 5 April 1927, herb. Kamamoto University (not seen); isoneotype MO-3961584 (digital image seen).

Plants yellowish green, in open to compact wefts, with a leafy creeping primary stem to 13 cm long, c. 170 μm diam., occasionally forked or with lateral branches; the primary stem giving rise to branches in a pinnate arrangement, although the arrangement is often obscured because the branches are turned to one side and grow away from the substrate. Branches densely leafy, 2–3 mm apart along stem, to 8 mm long but mostly < 6 mm, c. 115 μm diam., commonly with 1–8 elongate flagelliform branchlets up to 14 mm long projecting laterally from the branches, the branchlets fragile and deciduous; branchlets in various stages of development, from dormant buds to fully formed branchlets; branchlet junction subtended by a ring of scaly leaves. Secondary branches rare. Rhizoids brown, in fascicles at intervals along stem. Stem leaves ovate-lanceolate from a broader base, insertion narrow, occasionally somewhat auriculate, tapering to a long narrow point, concave, rather undulate and plicate when dry, less so when wet, (1.39) 1.82–1.91 × 0.47–0.63 mm; margin denticulate, almost smooth in upper leaf; costa narrow, failing in mid-leaf; laminal cells in mid-leaf elongate-fusiform, 54–64 × 4.5–6.4 μm, longer towards apex, forming a herringbone pattern under low power transmitted light because of the elongate ends of cells, 1–3-papillose on both adaxial and abaxial surfaces, papillae prominent, cells at extreme apex smooth. Branch leaves widely spreading, insertion U-shaped, clasping, ovate-lanceolate, tapering to a fine point, 1.6–1.8 × 0.69–0.86 mm near the branch base but often gradually becoming smaller distally so that the branch appears attenuate; margin denticulate, somewhat undulate when wet, leaf contorted and plicate when dry; costa narrow, ending above mid-leaf; laminal cells above leaf base elongate-fusiform, thin-walled, forming a herringbone pattern as in stem leaves, 1–2(–3)-papillose on both adaxial and abaxial surfaces, cells papillose to apex; median cells 41–64 × 4.4–6.4 μm; cells in leaf base rectangular, smooth. Flagelliform branchlet leaves appressed to branchlet stem when dry, spreading when wet, lanceolate with a long, narrow tip, 0.4–0.53 × 0.09–0.13 mm; insertion straight to curved, margin denticulate; costa very narrow, failing below midleaf, laminal cells fusiform, mostly unipapillose on both adaxial and abaxial surfaces (sometimes 2-papillose, rarely 3-papillose), 40–45 × 5–7 μm, those at the base rectangular, somewhat granular, smooth; apical cells linear, smooth.

Dioicous. Perichaetia not seen. Perigonia not seen.

Our observations and measurements of WT-637 agree broadly with those of *M. undulata* (CBG-8207146) and with descriptions published by Noguchi (1936, 1976), Manuel (1977), and Wu and Pei (2011). Differences in leaf or laminal cell sizes may be accounted for by environmental variation. Similarly, differences in colour — 'yellowish-green' (Noguchi 1936) and 'dark green' (Noguchi 1976) — probably reflect differences in light intensity in the habitat. The description that best matched WT-637 was that for Taiwanese specimens of *M. undulata* by Wu and Lin (1986), who illustrated the leaves of the flagelliform branchlets.

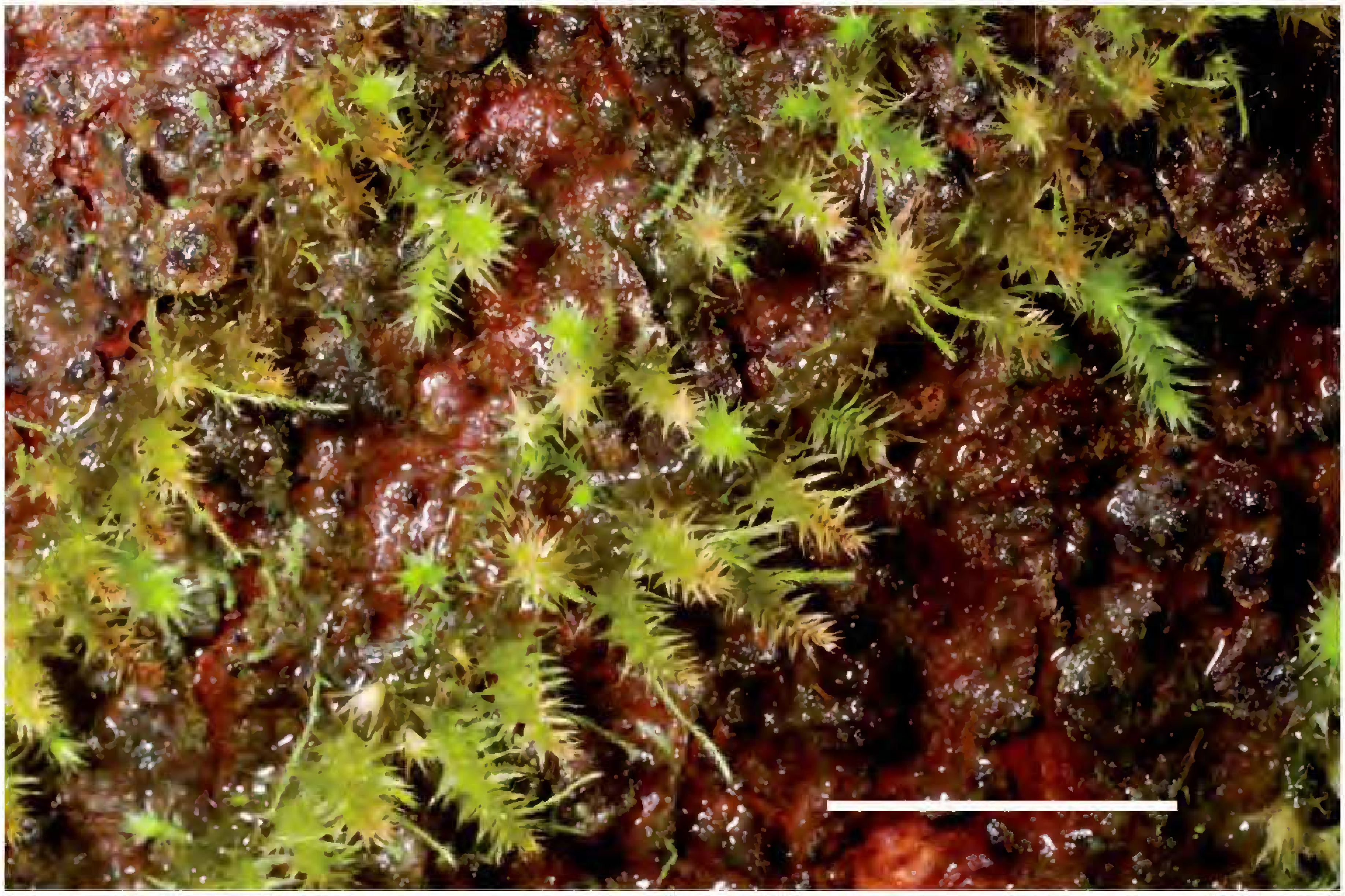

Fig. 1. *Meteoriopsis undulata* (WT-637) photographed *in situ* on the trunk of a tree, K-tree Track, Wooroonooran National Park, 29 May 2015. Scale bar: 10 mm.

Specimens of *Meteoriopsis undulata* examined: AUSTRALIA: QUEENSLAND: Cook: Wet Tropics: Tully Gorge National Park, H Road, on rotting vine, *Meagher & Cairns WT-616*, 27 May 2015 (BRI); Wooroonooran National Park, K-tree Track, epiphytic on tree trunk, *Meagher & Cairns WT-637*, 29 May 2015 (BRI). JAPAN: Shikoku: Tokushima-ken, Naka-gun, Aioi-cho, Hono, 130 m alt., on tree trunks, *Iwatsuki & Kiguchi, s.n.*, 28 August 1978 (CBG-8207146).

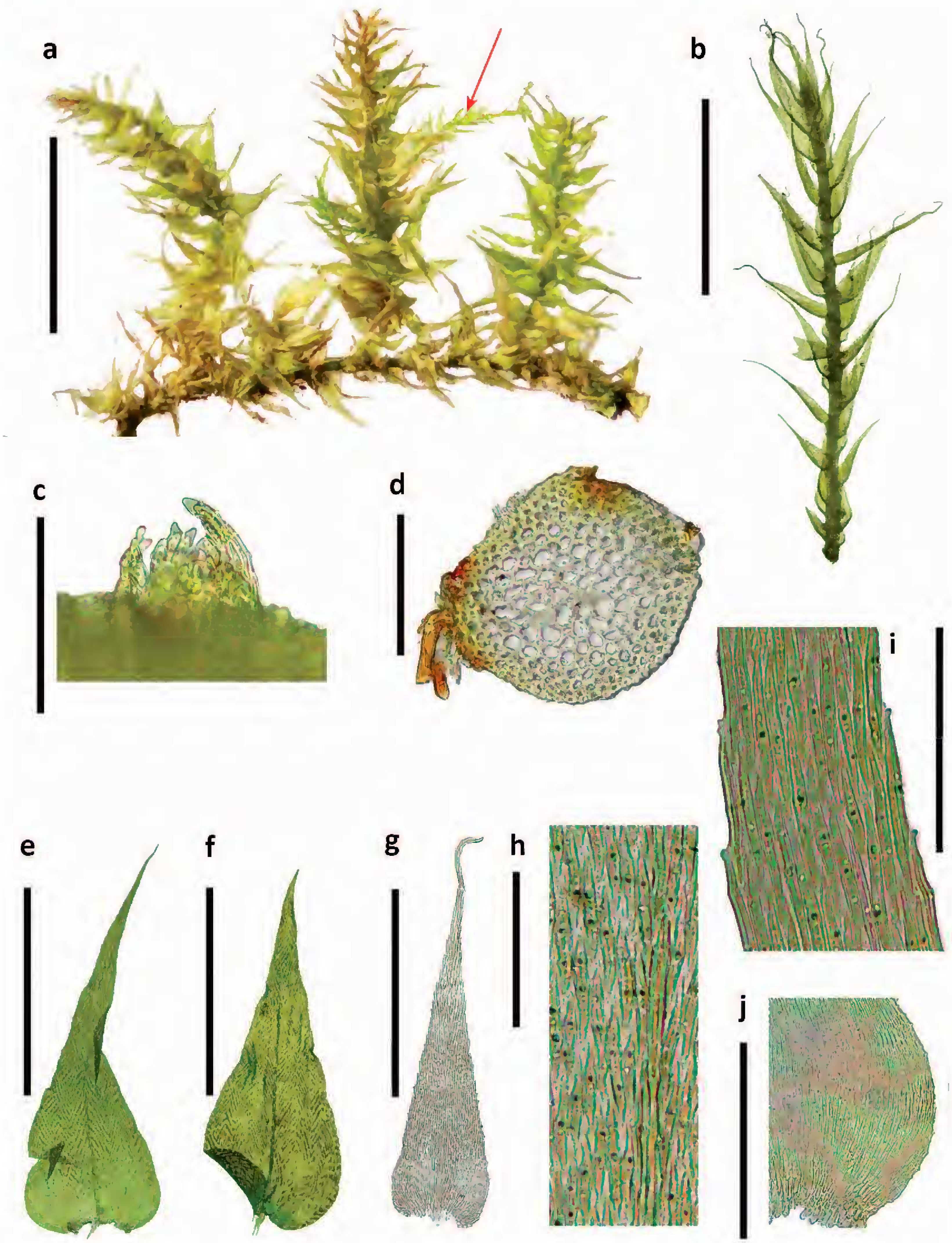

Fig. 2. *Meteoriopsis undulata*. **a,** part of plant with flagelliform branchlet (arrowed) arising from the middle branch; **b,** short flagelliform branchlet; **c,** scale leaves surrounding a branchlet junction; **d,** stem cross-section; **e,** typical stem leaf; **f,** typical branch leaf; **g,** typical flagelliform branchlet leaf; **h,** cells in centre of stem leaf, with end of costa visible on right; **i,** cells in the upper part of stem leaf; **j,** basal area of stem leaf showing denticulate margin and indistinct alar cells. Scale bars: a = 10 mm, b,e,f = 1 mm, c,d = 100 µm, e,f = 1 mm, g,j = 0.5 mm, h,i = 50 µm. All images from WT-637.

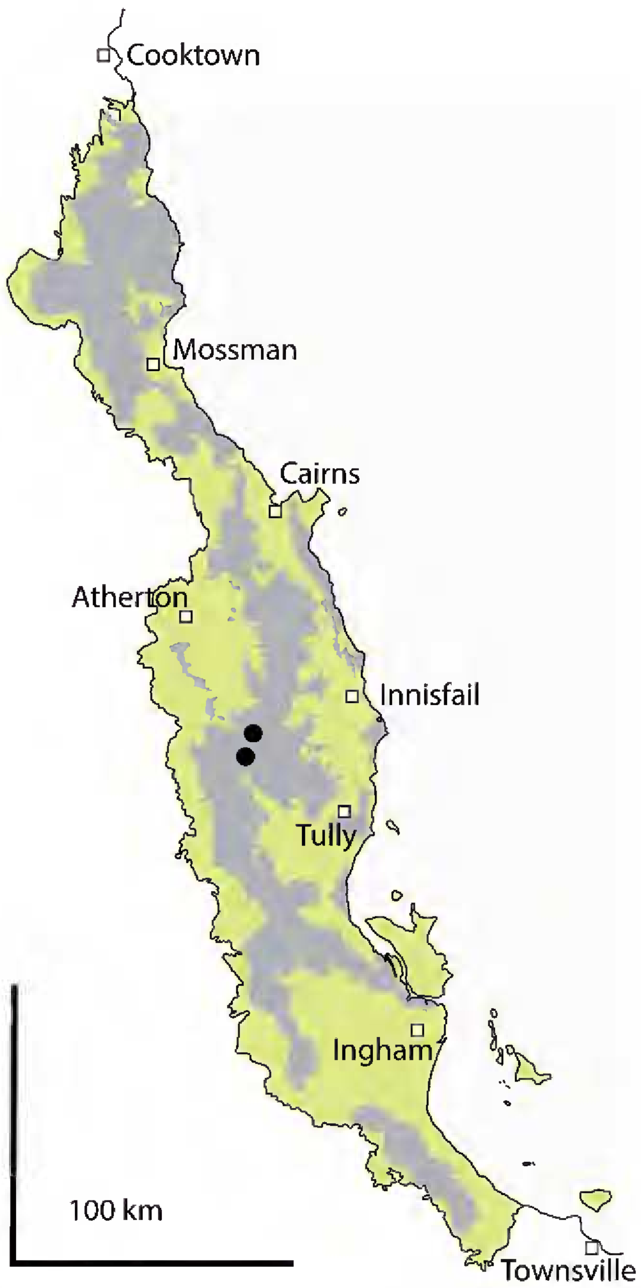

Fig. 3. The Australian Wet Tropics bioregion, showing the locations of collections of *Meteoriopsis undulata* (black circles). The Australian Wet Tropics World Heritage area is shown in grey.

Discussion

Papillosity: The laminal cells of WT-637 usually have one or two papillae on each side of the cell, and sometimes three on each side (Fig. 2h, i). This is consistent with Wu and Lin (1986) who reported '1–2 papillae, rarely 3 papillae per cell'. In his original description (1936) Noguchi recorded laminal cells as 'plerumque unipapillosae' – 'mostly unipapillose', suggesting some variation within the leaves he examined; however, Noguchi's later description stated only 'unipapillose' (Noguchi 1986). There is some variation in the description of papillosity in other species of *Meteoriopsis*. For example, Noguchi (1976) described laminal cells in *M. reclinata* as possessing one, rarely two papillae, whereas Streimann (1991, 2012) described the same species as having 1 (–3) papillae per cell – one high central papilla, rarely 2–3, or papillae indistinct. This disparity is not unusual; mosses commonly show morphological plasticity under varying environmental conditions (Buryova and Shaw 2005, Pereira et al. 2013). Variation is also common in other characters in *Meteoriopsis*; for example, Noguchi (1976) attributed variations in the length of the chain of linear cells at the leaf apex to an 'ecological feature'. However, he did not ascribe variations in papillosity to environmental effects, stating 'papillae may be a distinguishing character among taxa'.

Flagelliform branchlets: When Noguchi (1936) first described *Meteoriopsis undulata* he did not mention flagelliform branchlets, but later he described the species as having 'branches...often bearing long lateral flagella' (Noguchi 1986). Wu and Lin (1986) also mentioned 'lateral slender branchlets', suggesting they may be a kind of propagula, and illustrated leaves from these branchlets; nevertheless, the most recent description in the Moss Flora of China (Wu and Pei 2011) makes no mention of branchlets. Lateral flagelliform branchlets are a significant feature of WT-616 and WT-637 and can be seen clearly in the habitat photograph (Fig. 1). When we examined these specimens in a dried state several months after collection, many of the flagelliform branchlets had broken off and were loose within the packets, which suggests that they may act as deciduous vegetative propagules. The isoneotype of *Meteoriopsis undulata* (MO-3961584) has at least two flagelliform branchlets, one of which is separated from its branch. We also found several branchlets in the herbarium specimen of *M. undulata* (CBG-8207146), all separated from their branches and most somewhat longer than those in WT-637 but shorter than those in WT-616. It may be that the production of flagelliform branchlets is a seasonal phenomenon; deciduous branchlets might grow during the wet season before being dislodged by natural disturbance as they dry out later in the year.

Imura and Iwatsuki (1990) classified vegetative diaspores on a range of Japanese mosses and provided definitions to standardise terminology. They described one type of diaspore they termed 'flagella', defined by 'a slender, flagelliform, branch-like structure with small, suppressed leaves, often observed in axils of upper leaves of some mosses'. Because the basal connection of a flagellum consists of many cells, Imura and Iwatsuki (1990) considered flagella to be specialised branches. The basal connections in our material were difficult to observe when the flagella were in situ; however, the connections were clearly ringed by minute leaves (Fig. 2), which supports the idea that flagella are specialised branches.

Floribundaria walkeri (Renauld & Cardot) Broth., a moderately common species of Meteoriaceae in the Wet Tropics, can have flagellate branches, but the flagella are extensions of branches rather than specialised branches, and the plants have a soft, silky appearance.

Scaly leaves or pseudoparaphyllia?: WT-616 and WT-637 have numerous branches bearing flagelliform branchlets in various stages of development in leaf axils. Other branches have small buds towards the ends of some of the branches (Fig. 2c), and others lack buds or bear developing flagelliform branchlets. In mosses, branches that develop in the axils of stem leaves are often protected by axillary hairs and proximity to the leaf, whereas lateral branch buds are often covered by modified leaves for their protection (Akiyama 1990). Dormant branch buds may be protected by pseudoparaphyllia, which are derived from stem epidermal cells, or by scaly leaves, which are derived from cells of the branch primordia (Akiyama and Ishimura 1993). Because branching in WT-616 and WT-637 is mostly pinnate, we think that the buds must be dormant flagelliform branchlet buds.

Akiyama and Nishimura (1993) recognised that pseudoparaphyllia are taxonomically useful but acknowledged that there has been difficulty distinguishing them from scaly or rudimentary leaves. In his search for pseudoparaphyllia in a variety of North American mosses, Ireland (1971) found no pseudoparaphyllia in three genera in the Meteoriaceae: *Barbella*, *Meteoriopsis*, and *Papillaria*. Allen (1987) surveyed branch primordia in Pterobryaceae and compared them with Meteoriaceae. He found that Pterobryaceae commonly have pseudoparaphyllia, whereas they are absent in Meteoriaceae. He cautioned that 'a fine line exists between foliose pseudoparaphyllia and rudimentary branch leaves' and 'distinguishing between [them] can be a formidable task'.

Bruce Allen, at the herbarium of the Missouri Botanical Garden (MO), advised us that the herbarium has a duplicate specimen (MO-2854950) of the material of *M. undulata* we borrowed from Canberra, as well as an isoneotype of *M. undulata*. After viewing our photos of WT-637 and comparing them with the specimen in MO, he concluded that *M. undulata* has scale (rudimentary) leaves around branch primordia, and not foliose pseudoparaphyllia (pers. comm. B. Allen, December 2015).

The production of vegetative propagules in dioicous mosses may compensate for the absence of one gender in a population (Glime and Bisang 2014a,b). In this respect it is noteworthy that perichaetia are lacking in WT-616, WT-637 and CBG-8207146, although there are a few perichaetia in MO-2854950 (pers. comm. B. Allen, January 2016).

Perichaetia and perigonia: Manuel (1977) noted that in *Meteoriopsis* the perichaetia are terminal on short branches arising from the primary stem, and are inconspicuous; perigonia are sessile in the axils of leaves on pendent stems, and are conspicuous. Both perichaetia and perigonia have long paraphyses. He also noted that he had not seen perichaetia or perigonia on any specimen of *M. undulata* (all from Japan), and that in *M. reclinata* and *M. squarrosa* perichaetia were rare.

Noguchi (1976), who examined specimens of *M. undulata* from Taiwan, found perichaetia but not sporophytes. Wu and Lin (1986) also found perichaetia, and gave the only description of the perichaetial leaves: lanceolate to linear, broader at the base, apex slightly curved, about 1.5–2.4 × 0.2–0.4 mm. However, they did not describe archegonia or paraphyses. WT-616 and WT-637 do not bear perichaetia or perigonia. Reproduction in *M. undulata*, but not necessarily *Meteoriopsis* in general, therefore appears to be primarily if not wholly asexual by fragmentation.

Disjunct distribution: The Wet Tropics of northern Queensland is an outlier in the known distribution of numerous Asian bryophytes such as *Meteoriopsis undulata* (Fig. 4). Two other examples are *Entodontopsis pygmaea* (Paris & Broth.) W.R.Buck & Ireland (otherwise known from Vietnam, Thailand, China, India and Nepal) and *Bazzania bilobata* N.Kitag. (otherwise known from Thailand and China). However, these might not represent genuinely disjunct distributions, because bryophytes are poorly known in many parts of the South East Asian archipelago. For example, there are very few collections from Indonesia's Irian Jaya, which covers the entire western half of New Guinea. Potential natural vectors for the long-distance dispersal of bryophyte diaspores in the Asian–Australasian tropics include cyclones, migrating birds and fruit bats.

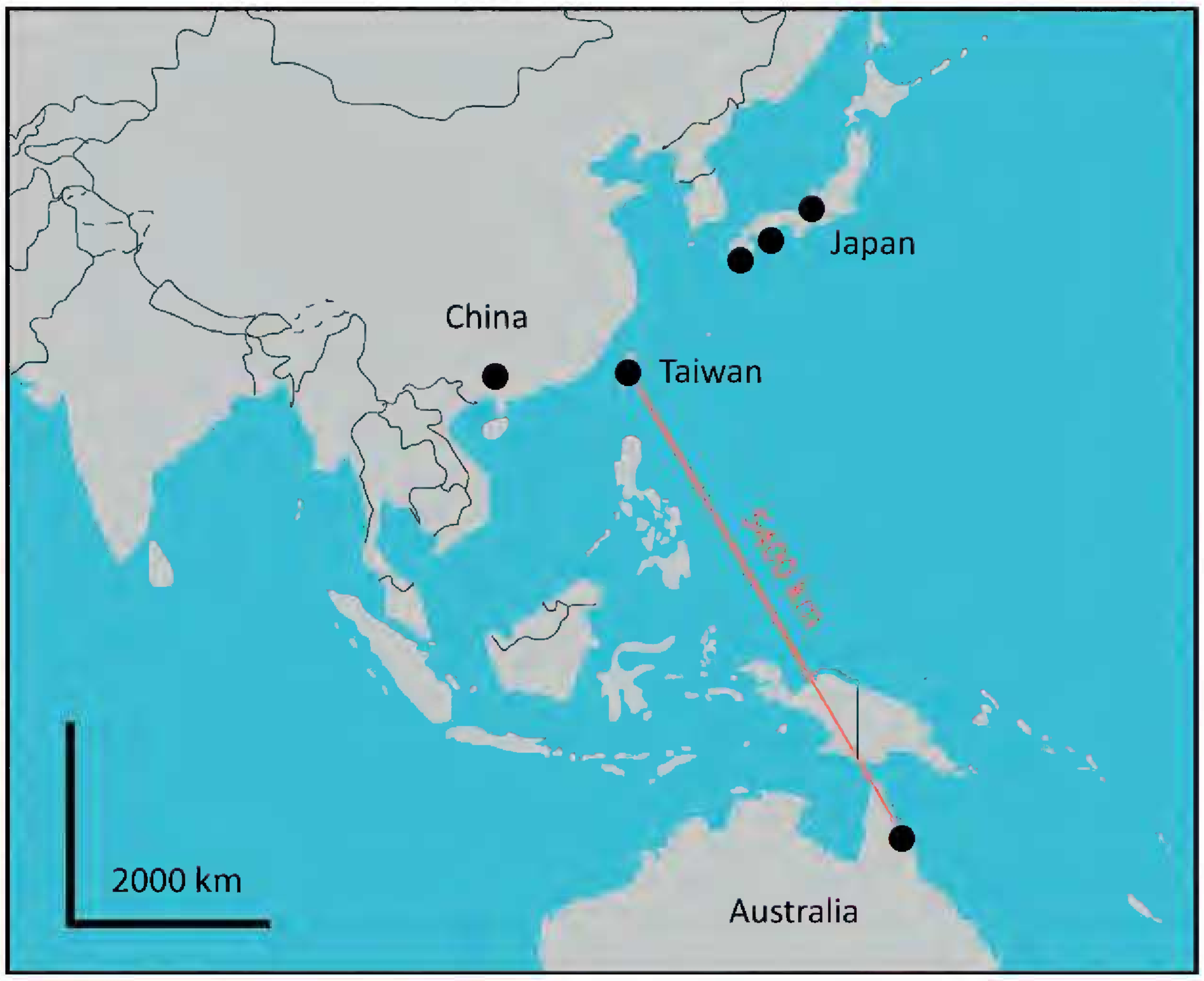

Fig. 4. The known global distribution of *Meteoriopsis undulata*, showing the disjunction of the Wet Tropics sites.

Position in the Australian moss key: Two versions of the Australian moss key have been published. The earlier version (Buck et al. 2002) was superseded by a revised version (Buck and Vitt 2006), which is available online and should be the version used to identify Australian mosses to genus. The following notes refer only to Buck and Vitt (2006).

Meteoriopsis as currently accepted in the Australian flora (i.e. *Meteoriopsis reclinata*) keys out at couplet 218, but to arrive there one must accept that the cells are unipapillose. Since in *M. undulata* they are very commonly 2–3-papillose as well as unipapillose, allowance needs to be made for *Meteoriopsis* to key out further along in the key. In addition, *Floribundaria walkeri* might not be keyed correctly because its cells typically have the papillae in two rows, rather than one as suggested by 'Laminal cells seriately papillose' in couplet 229 of the existing key. We therefore suggest the following replacement for the existing couplet 229:

229 Plants with caducous flagelliform branchlets arising ± at right angles from branches, the junctions surrounded by minute leaf-like scales... ***Meteoriopsis***

229: Plants lacking flagelliform branchlets as above (although branches may be terminally flagellate)........... .... 229A

229A Laminal cells seriately papillose in 1 or 2 rows... ***Floribundaria***

229A: Laminal cells with papillae scattered over the lumina... 230

Conclusion

WT-616 and WT-637 are more or less identical to *Meteoriopsis undulata* Horik. & Nog. as identified by Iwatsuki for CBG-8207146 and described by Wu and Lin (1986), and we therefore identify them as that species. As Manuel (1977) and Wu and Pei (2011) did not mention flagella in their descriptions, flagella may have been absent when their specimens were collected or lost during repackaging of dried material. Alternatively, the production of flagella may be initiated by an environmental trigger that had not occurred for plants they examined.

A study of *Meteoriopsis* from the South East Asian archipelago (particularly Borneo, Sumatra, Celebes and Papua New Guinea), including numerous specimens unidentified to species level in Australian herbaria, would help to refine the delimitation of species and determine whether the Wet Tropics is a genuinely large disjunction in the distribution of *M. undulata*.

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